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Investigational Report No. 7

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PRELIMINARY INVESTIGATIONS ON THE HEARING OF SHARKS

by

D. H. Davies*, J. P. A. Lochner† and E. D. Smith†

ABSTRACT

A NUMBER of sharks, including *Carcharinus obscurus*, *C.maculipinnis*, *C.leucas* and *Sphyrna lewini* were conditioned to respond to pure tones and octave bands of random noise and their thresholds of hearing were determined for these stimuli. The results obtained suggest that sharks are not able to discriminate between frequencies and that their recognition of signals is based on the amplitude versus time characteristics of these signals. They can apparently determine the direction of a sound source accurately.

1. INTRODUCTION

THE INCIDENCE of shark attack on humans off the east coast of the Republic of South Africa is high. Fifty-nine attacks have occurred since 1940 and of these twenty-four were fatal and the others caused gross physical injuries.

The present work on the hearing of sharks is being carried out at the Oceanographic Research Institute in Durban as part of a programme of investigation into the biology and behaviour of sharks with the ultimate object of devising a means of protecting humans from shark attack.

Very little is known about the hearing ability of sharks and it was considered that the most reasonable means for learning more about their hearing was to condition them to respond to sound and to analyse their response to different types of sound stimuli. As far as we know, there are four precedents for the conditioning of sharks to sound stimuli. Vilstrup (1) conditioned Spiny Dogfish (*Squalus acanthias*) to a motor horn, Moulton (2) demonstrated the ability of the Smooth Dogfish (*Mustelus canis*) to associate an oscillator signal with an electric shock, Clark (3) showed that an operant response could be elicited from large Lemon Sharks (*Negaprion brevirostris*) and Kritzler and Wood (4) obtained a provisional audiogram for the Bull Shark (*Carcharinus leucas*).

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During the present experiments a group of young sharks including *Carcharinus obscurus*, *C.maculipinnis*, *C.leucas* and *Sphyrna lewini* were conditioned to respond to pure tones and to bands of random noise. Audiograms were determined for these two types of stimuli in the presence of background noise that existed in the tank. Some interesting conclusions can be drawn from the results obtained.

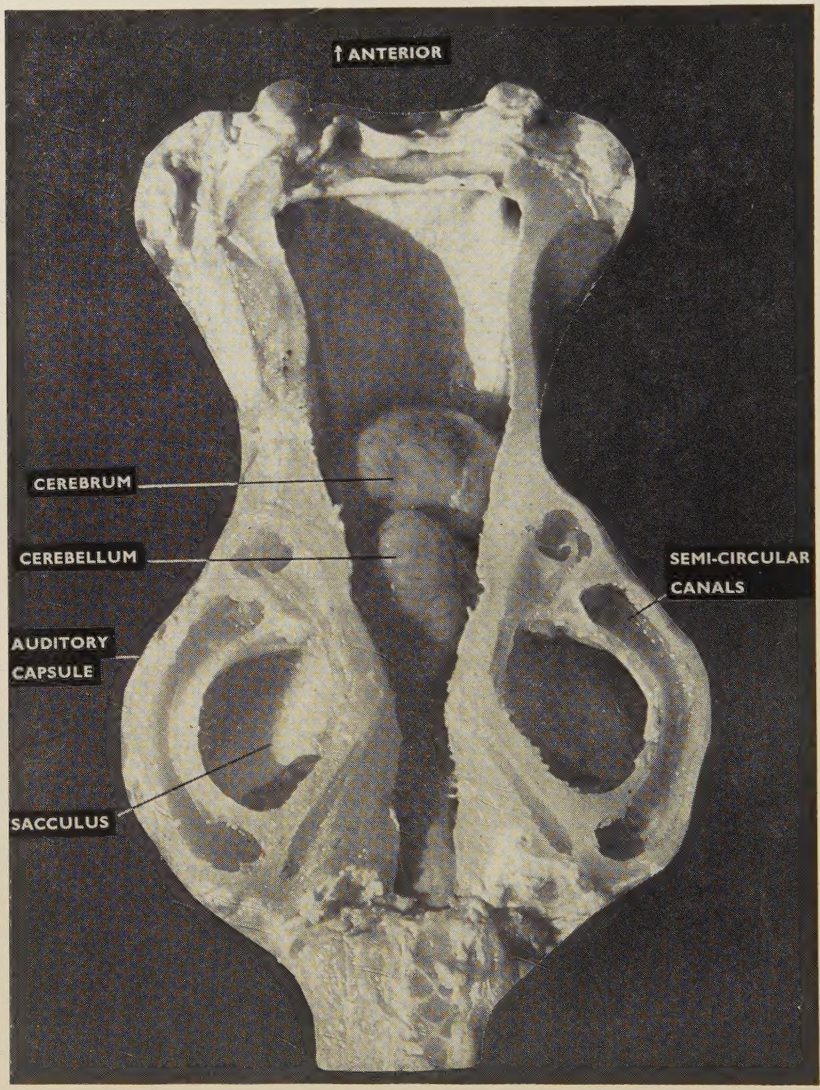

FIG. 1. Dorsal view of partly dissected Chondrocranium of *Carcharinus limbatus*.

2. HEARING MECHANISM OF THE SHARK

In the elasmobranchs there is no equivalent of the outer and middle ear of humans. The inner ear is housed in the cartilaginous auditory capsule of the chondrocranium and consists of the anterior, posterior and horizontal semi-circular canals together with the *utriculus*, the *sacculus* and an outgrowth from the posterior ventral region of the sacculus called the *lagena* (see Figs. 1 and 2).

The sacculus, which is generally regarded as the principal organ of hearing, is in the form of a flat vesicle suspended across the auditory capsule which is filled with large numbers of minute calcareous particles — the otoliths, and clear fluid — the endolymph. The otoliths form a heavy, white paste of S.G. 1.88. The perilymphatic space is irregularly traversed by strands of connective tissue (*trabeculae*) which carry small blood vessels and also suspend the membranous labyrinth. The labyrinth is connected with the exterior via the endolymphatic ducts which lead to the utriculus.

In the utriculus and sacculus are areas of receptor cells called *maculae*. The maculae consist of a neuroepithelium composed of supporting cells and neuromast cells the hairs of which are ensheathed in a gelatinous pad, the cupula. These cells are innervated by nerve fibres which ultimately join the VIIIth nerve.

In their electrophysiological experiments on the Ray (*Raja*) Lowenstein and Roberts (5) found that propagated impulse dis-

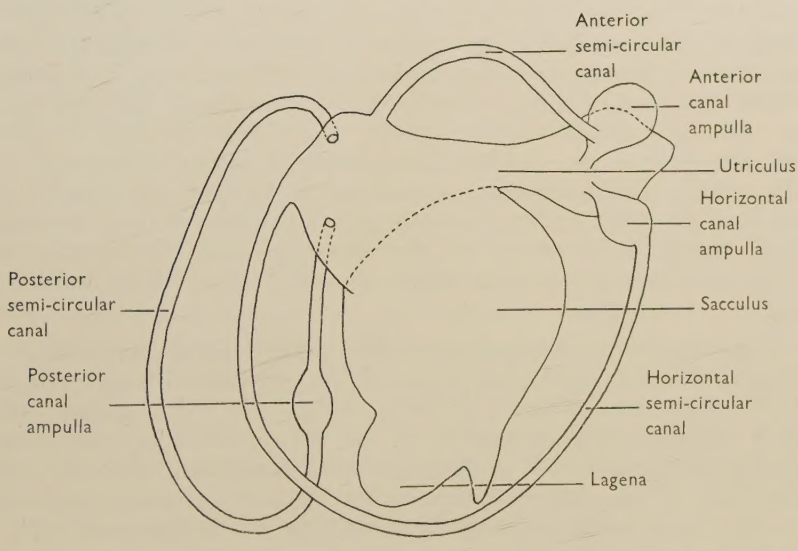

FIG. 2. Diagram showing lateral view of the right auditory region of *Carcharinus obscurus*.

charges (or action potentials) in response to low frequency vibratory stimulation (up to 120 c.p.s.) were recorded from nerve twigs in the anterior region of the sacculus, from a part of the utriculus and from the roof of the sacculus cavity. Similar responses were not found in the lagena which (in the Ray) was found to contain gravity receptors only.

3. THE HEARING PROCESS

VERY LITTLE is known about the hearing process of sharks but it appears to differ widely from and to be considerably less complex than that of humans.

The basic difference may be attributed to the fact that human hearing takes place in air while elasmobranch hearing takes place in water. The requirements of sharks in relation to impedance-matching devices and mechanisms for the determination of direction are therefore entirely different to those of humans.

In humans the paired ears are pressure operated devices and direction is obtained from the difference in time of arrival of sound pulses at each of the two ears. In view of the close proximity of the paired auditory capsules of sharks the same process could not be used since the velocity of sound is much higher in water than in air and the difference in time of arrival is correspondingly very much reduced.

A study of the gross anatomy of the auditory system of sharks and of their response to sound stimuli has suggested certain possibilities in relation to their hearing. The indications are that the paired auditory organs of sharks (*sacculi*) are velocity operated devices. The cartilaginous auditory capsule is probably well matched to the surrounding medium of sea water and it is likely that it vibrates with approximately the same amplitude and direction as the water particles when sound waves pass through it. The heavier material in the sacculus presents a higher impedance to the wave and a pressure proportional to the particle velocity is generated on the auditory membrane. This pressure is converted into electrical potentials by the receptor cells which in turn trigger the action potentials which are transmitted by the auditory nerve to the brain.

It is likely that the elasmobranch auditory system, as a velocity operated device, has typical figure eight responses with zero points in the plane of the auditory vesicle or *sacculus*. The *sacculus* lies in a plane at approximately 130° to the direction of swimming and approximately 45° to the horizontal in the case of *C.limbatus* (see Fig. 1). This means that when the shark is swimming towards a sound source the intensity in its left ear will be increased when it turns its head to the right, while the intensity in its right ear will be decreased. The opposite happens when it turns its head to

the left. During normal swimming motions the head of a shark moves slightly from left to right in a scanning motion which should greatly facilitate its ability to follow a sound source. It should also be possible for the shark to follow a sound source in azimuth because of the probable presence of a zero at an angle of approximately 45° from the horizontal in the direction of swimming.

It is difficult to understand how antero-posterior discrimination is obtained with paired velocity-type hearing mechanisms but this problem has not been satisfactorily solved even for the human hearing system, which employs paired pressure-type hearing mechanisms. It is possible however, that the shark might make use of a combination of velocity and pressure sensitive devices to overcome this difficulty.

With this type of hearing mechanism, sharks could be expected to have a rather flat frequency response over a relatively wide frequency range.

It seems most unlikely that sharks are able to discriminate frequencies or pitch as they apparently possess no organ equivalent to the basilar membrane, which is responsible for frequency discrimination in the human.

4. EXPERIMENTAL FACILITIES

THE PRESENT experiments were carried out in a concrete tank 45ft. long, 30ft. wide and 10ft. deep containing 85,000 gallons of sea water which has a continuous circulation providing a total replacement of the entire contents of the tank every five hours.

Two galleries surround the tank, one at surface level and the other below the surface containing 22 large viewing windows arranged round the sides of the tank. These provide excellent below surface viewing of the sharks from all sides.

The pure tone and random noise sound signals were generated by appropriate electronic circuits and introduced into the tank through a small underwater loudspeaker permanently installed in a convenient position near the overflow weir of the tank. The intensity of the sound field in the tank was obtained by calibrating the equipment against a calibrated hydrophone.

It was found that a fairly uniform field could be obtained when bands of random noise were used as sound stimuli but that severe standing waves were obtained when pure tones were used. To overcome this difficulty the average of the pressure maxima was regarded as representing the field intensity as it was argued that the sharks would pick up peak intensities (either in the form of pressures or velocities) while swimming in the tank.

A telegraph key, for sounding the loudspeaker, was installed at the window nearest to the underwater loudspeaker so that the

operator could observe the response of the sharks after he had given the signal. The observer was in telephonic communication with the person responsible for the feeding of the sharks from the upper gallery.

FIG. 3. *Carcharinus obscurus* feeding after presentation of sound signal in Shark Research Tank.

5. CONDITIONING OF SHARKS

A COLLECTION of 25 - 30 young sharks, of the four species mentioned below was placed in the Shark Research Tank of the Oceanographic Reasearch Institute in Durban and conditioned to respond to sound signals from a small underwater loudspeaker. This was possible only after the sharks had begun to accept food presented in the form of cut pieces of tuna of approximate weight 100 gm. Each time food was presented, a pure tone signal of 500 c.p.s. was given.

This procedure was repeated in the early morning of every third day as the sharks would not eat readily at shorter intervals. After 6 - 10 presentations it was found that sharks in the far end of the tank turned sharply towards the loudspeaker when the signal was given. At this stage the procedure was modified in such a way that the signal was sounded first and only when a group of sharks had turned and had begun to congregate near the loudspeaker was food introduced by an unseen operator from the top gallery, (see Fig. 3).

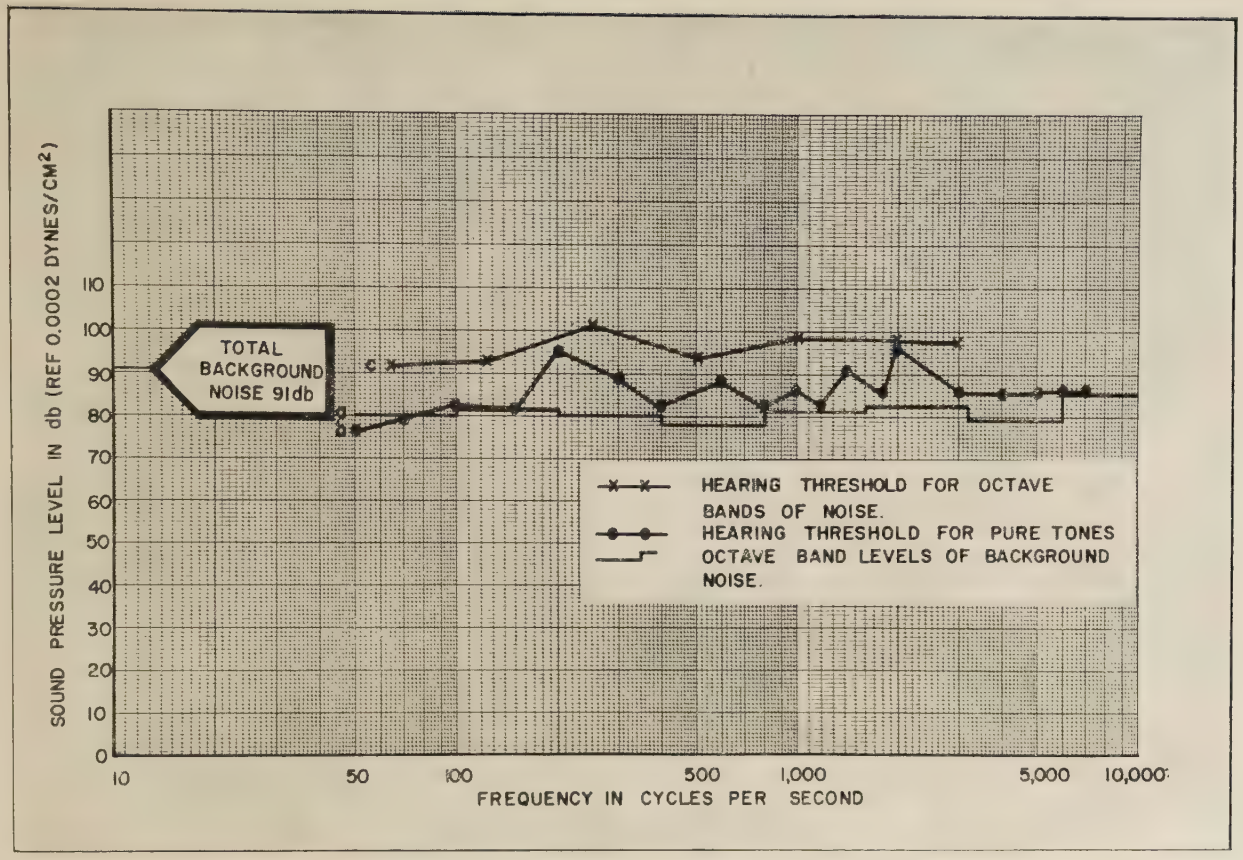

FIG. 4. Thresholds of hearing for octave bands of noise, pure tones and octave band levels of background noise.

In this manner excellent conditioned response was obtained within a month after the first presentation, from a group of young sharks of the following species:

Dusky Shark *Carcharinus obscurus;* Black-tipped Shark *C.maculipinnis;* Zambezi Shark *C.leucas;* and Hammerhead Shark *Sphyrna lewini.* The length of the young sharks varied from 2 - 4ft. and the weight from 5 - 25lbs.

These sharks were subsequently conditioned to respond to pure tones over a frequency range of 50 - 7,000 c.p.s. and to octave bands with mid-frequencies varying from 64 - 3,000 c.p.s. with the object of determining their threshold of hearing over these frequency ranges.

6. RESULTS OBTAINED

THE BACKGROUND noise in the shark research tank was measured and found to have a level of 91 dB relative to 0.0002 dynes per cm^2. The octave band levels of this noise are given by curve (a) of Fig. 4.

The sharks in the tank were first conditioned to respond to pure tones and the intensities of these tones at the different frequencies were reduced in steps of 5 dB until no response was obtained. The lowest intensities at which sharks responded were regarded as their threshold of hearing. Curve (b) in Fig. 4 is the pure tone threshold curve for the sharks tested. The irregularity of this curve is probably due to mechanical resonances of the loudspeaker and to standing waves in the tank.

The sharks were then conditioned to respond to octave bands of random noise and their thresholds determined for the different bands. Curve (c) of Fig. 4 gives the octave band threshold contour obtained for the sharks in the tank.

During the tests it was noticed that sharks conditioned to a pure tone at one frequency would also respond to pure tones at other frequencies and sharks conditioned to random noise in one frequency band would also respond to random noise in other frequency bands, provided the frequency difference was not too great. It was observed that sharks conditioned to an octave band with a mid-frequency of 3,000 c.p.s. did not respond to a band at 500 c.p.s. but did respond to a band at 1,000 c.p.s. It was also found that sharks conditioned to pure tones respond to bands of random noise but sharks conditioned to bands of random noise do not respond to pure tones even at the mid-band frequencies.

This suggests that the sharks have been conditioned to respond to the amplitude versus time characteristics of the signal and not to the amplitude versus frequency characteristics of the signal.

During the tests the underwater loudspeaker was moved to a different position and it was noticed that the sharks went to the loudspeaker when it was sounded and not to the position where it was usually placed.

7. CONCLUSIONS

As a result of the present studies the following conclusions can be drawn:

(i) It is readily possible to condition sharks of a number of species to respond to sound stimuli.

(ii) Sharks respond to sound stimuli over a wide frequency range the limits of which have not yet been determined.

(iii) The physiology of the hearing mechanism as well as responses obtained, suggest that sharks cannot discriminate between frequencies but that they are able to discriminate between signals by the recognition of amplitude versus time patterns.

(iv) The threshold curve obtained for pure tones is very similar to the curve obtained for bands of random noise. This suggests that the hearing mechanism of the shark is a simple amplitude detector. It appears that the thresholds are masked at a level which is determined by the R.M.S. value of the background noise. At lower ambient noise levels the thresholds will undoubtedly be lower.

(v) Sharks are capable of accurate determination of the direction from which sounds originate. A preliminary study of the gross anatomy of the sound perceptors leads us to believe that the hearing system of the shark is a velocity-operated mechanism and that the perception of direction is based on the directional characteristics of the auditory organs themselves.

(vi) The preliminary results obtained suggest that much could be learned about the hearing of sharks by a thorough electro-physiological investigation of the hearing mechanism.

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